THE REPRODUCTIVE ECOLOGY OF *EUSCORPIUS FLAVICAUDIS* IN ENGLAND

T.G. BENTON

The reproductive ecology of the scorpion *Euscorpius flavicaudis* was studied both in the field in England (at a colony dating back 120 yrs), and under semi-natural conditions in the laboratory. Before the mating season males become vagrant to search for females. On encountering a pregnant female or one with young, in her 'burrow', the male may mate-guard her until her period of maternal care ends and she becomes receptive to him. Large males have a higher mating success than small males. Two instars of adult males exist in this population of scorpions: large 7th instars and small 6th instars, and the reasons for this apparently paradoxical situation are explored. □*Euscorpius, mate-guarding, mating, life-history.*

T.G. Benton, Department of Zoology, University of Cambridge, Downing St., Cambridge, CB2 3EJ, United Kingdom; present address: School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, United Kingdom; 7 December, 1992.

Evolutionary and behavioural ecology are relatively young disciplines; and have to date concentrated on using the more 'familiar' animals as subjects: birds, mammals and insects. These disciplines have largely passed arachnids by. Increasingly, however, we are beginning to realise the utility of arachnids as model animals in helping to elucidate general evolutionary principles.

Although there has been considerable increase in behavioural ecological interest in spiders in recent years, scorpions have been largely ignored. This is perhaps because they are difficult animals with which to work – long-lived, inactive, elusive and nocturnal. This paper outlines some of the main findings of a study of scorpion reproductive ecology. It is unfortunately incomplete; posing more questions than it solves; but, I hope that it illustrates the fact that, as in so many areas of their biology, scorpions are idiosyncratic, fascinating and more complex than they may first appear. This study combines the power of controlled laboratory experiments and the ease of laboratory observations with the reality of what is observed in the field; and, by so doing, for the first time the events surrounding the courtship of a scorpion are explored and placed in an ecological context.

THE STUDY ANIMAL

Euscorpius flavicaudis (de Geer), common throughout southern Europe (Birula, 1917), also occurs in England, most probably as a result of introductions. This species is a successful colonising species (Fage, 1928; Wanless, 1977; Lourenco & Vachon, 1981) and is often found associated with buildings (Wanless, 1977). Colonies have been reported from several locations in England, but only one, at Sheerness Docks, Kent (51°26'N, 0°45'E) has lasted many years and is of considerable size. The first record of scorpions at Sheerness is a label on a specimen of *Euscorpius flavicaudis* in the Natural History Museum, London: 'Taken in Sheerness Dockyard, 1870, J.J. Walker' (P.D. Hillyard, *in lit.*).

METHODS

FIELD OBSERVATIONS

At Sheerness Docks, most present buildings and the perimeter wall date from 1823 (Benton, 1992a). Scorpions are common in areas little frequented by people; and are especially common living in the perimeter wall. This old wall is about 4m high and 66cm thick. It shows the effects of time, with the mortar between the bricks crumbling away, creating 'cracks' which the scorpions readily inhabit. My study area was a 104m length of perimeter wall (bounding ornamental and vegetable gardens). The field study was conducted from January 1988 to July 1989, during which 92 visits were made to Sheerness Docks (totaling 500 hours of observations). Scorpions were observed using a portable ultra-violet light. Benton (1992a) details field methods.

LABORATORY OBSERVATIONS

To allow more complete observations and experimentation a laboratory colony of *Euscorpius* was set up, modelled on the habitat at Sheerness. This consisted of a plywood wall (2.44m x 5.79m), covered in sandpaper, with 144 slots (2.5

x 5.1cm) cut into the face. Into these slots were fitted artificial 'cracks' 12 cm long. These were open to the wall and closed at the far end. A layer of soil was placed at the base of the wall. This soil was periodically damped to mimic rain; and each week woodlice (the scorpion's natural food) were released onto it. This colony was kept under a natural photoperiod, and as near natural temperature and humidity as possible. Observations and experiments were conducted at night, when the wall was illuminated by lamps fitted with deep-red filters (invisible to scorpions: Machan, 1968). Unless being used in an experiment, the scorpions (collected at Sheerness) were allowed to move freely around the wall. Benton (1991a) details colony setup.

EXPERIMENTAL METHODS

In this study of male contest behaviour for females during the mating season, 11 males were used. On the artificial wall 40 x 40cm enclosures were made around a single crack. A female carrying young was placed in this crack, and later an experimental male was added. Thirty minutes after this male had encountered and entered the crack a second male was added. After encountering the crack the second male would attempt to enter. The males would then meet, assess each other and fight. This procedure was then immediately repeated. The two replicates constituted a 'contest' (and in all cases the results were unambiguous, and identical for each replicate). In total 110 contests were conducted (with each male as 'owner' against every other male as intruder). Contest order was randomly selected. Other methods are detailed in Benton (1992b), and scorpion mensuration in Benton (1991b).

RESULTS

BACKGROUND

Like most scorpions, *E. flavicaudis* is nocturnal. During the day and over the winter, they are not visible as they have retreated to the back of their cracks in the wall. At night, depending on the season, most scorpions evident are at the entrance to their cracks where they remain immobile, with their claws outstretched and open. The most common prey items are isopods (*Porcellio scaber*) (64%) and then conspecifics (12%) (Benton, 1992a).

SEASONS

Scorpion activity at Sheerness is highly seasonal. Over the winter very few (if any) can be seen. The numbers build up during the spring and peak in late summer (Benton, 1992a) before decreasing again to winter levels. As these scorpions live for several years (Benton, 1991b) this pattern reflects varying patterns of behaviour, rather than gross mortality and natality. For most of the year, most scorpions seen are in their crack (for November to June only $8 \pm 11\%$ of all scorpions observed are out of their cracks). However, in summer, on average, $24 \pm 9\%$ of scorpions observed were on the wall surface. Adult males make up most surface-active animals: 3-4x more males are seen on the wall surface than adult females over the summer (Figs 1a, b).

The number of females giving birth or with young peaks when female activity on the wall surface (Fig. 1a) is least. Females with young remain deep within their cracks, and were never observed to venture onto the wall surface. Indeed, females in the last stages of pregnancy also appeared to show a marked reduction in activity.

Most matings at Sheerness (Fig. 1b) are just after the number of females with young peaks (Fig. 1a). Known females with young were found to be unreceptive to males until 2 ± 1.2 days (n=12) after the juveniles had moulted and climbed off her dorsum (Benton, 1992b).

About 3 weeks after male surface-activity begins, the number of matings observed peaks (Fig. 1b). Only at this time can males and females be found together in the same crack. These periods of cohabitation averaged 10 ± 9.9 nights (range 1-30; n=19; data from field). Cohabiting occurred only prior to mating, and whilst the female was either carrying young, or in late pregnancy (Benton, 1992b). Males were associated sometimes with females living in shallow cracks (n=3); in which case the males spent the day in a deep crack nearby and 'commuted' to the female's crack to spend the night sitting at the entrance. The identity of the male mating with a specific female was known for 15 cases of cohabitation: in 14 the male had been recently cohabiting (P<0.005) with that female. Females of this species do not appear to assess males, and will mate with any male present when they become receptive (Benton, 1992b). If a male's encounter rate with females is low, and a female's receptivity is predictable, then a male encountering a soon-to-be receptive female may do better waiting for her to become receptive, rather than leaving her and risking trying to find a female nearer receptivity (Grafen and Ridley, 1983); and this seems to be the case with these scorpions (Benton, 1992b). This behaviour can also benefit
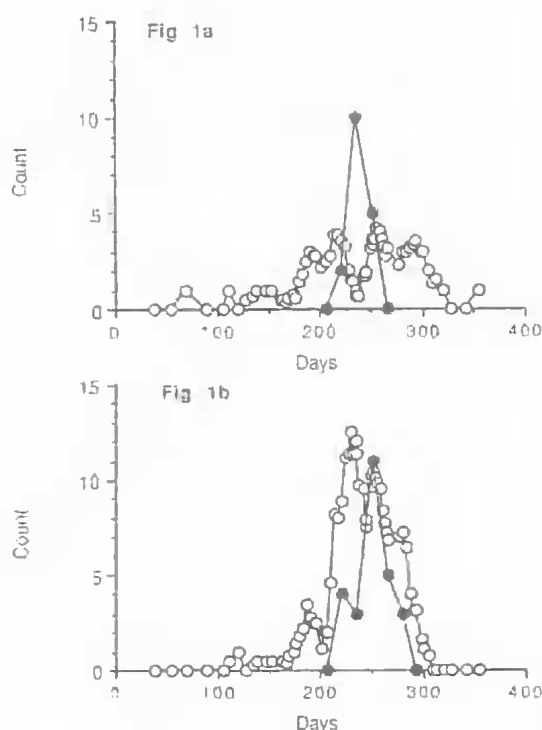
FIG. 1. Reproductive season of *Euscorpius flavicaudis* in England, 1988. (a) Seasonality of adult female surface-activity and no. of births. Female surface-activity is smoothed over two weeks: nightly count shown as average of preceeding and following week's counts. No. of births (for each half-month) estimated from no. of females giving maternal care, and date at which this ended. (b) Seasonality of adult male surface-activity (smoothed over two-weeks), and half-monthly count of no. of matings (observed no. of matings plus no. of spermatophores found). Data originally, in part, in Benton 1992b.

the females for two reasons. Firstly, it ensures that they are mated. Secondly, a major advantage of maternal care in scorpions is to prevent predation of the juveniles (Benton, 1991a), so having a male at the front of the crack prevents entrance by other scorpions which may aid this role.

In all cases of cohabitation, the male stations himself near the entrance, with the female behind him. Males attempting to enter the crack encounter the currently cohabiting males, and each tries to grasp the other's claws. Within a very few seconds one male retreats and flees from the crack. Males therefore fight for 'possession' of a crack occupied by a female in the period before she becomes receptive.

To investigate male mate-guarding contests 110 contests were staged between 11 males (each male as 'owner' against each of the others as 'intruder'). The proportion of contests won correlated very strongly with measures of scorpions size, and most strongly with pedipalpal claw length (r_s=0.97, P<0.001). This is to be expected as *E. flavicaudis* uses its claws as its main offensive weapon. In 80% of contests, the larger-clawed male won; when the smaller-clawed male won (20%), it was the 'owner' in most (91%) contests. Both relative claw-size and ownership status had highly significant effects on contest outcome (two-way ANOVA, size: F=68.5; df 1,36; P<0.0001; status: F=42.7; df 1,36; P<0.0001): large-clawed males usually won contests, but if contestants were closely matched in size then ownership status decided the outcome (giving an advantage equivalent to about 11% longer claws).

SIZE AND SEXUAL ADVANTAGE

In the laboratory, males differed in reproductive success: some males mated twice, some once and some not at all. Larger males mated more often than small males (Fig. 2). This size advantage is for two reasons. Firstly, as described above, larger males are better competitors for female-occupied cracks. Secondly, about 40% of matings are not preceded by mate-guarding. These fall into three broad categories: non-pregnant females at the start of summer, females not found by males before their maternal care has ended and (most rarely) females who have mated already (this is possible as a spermatocleutrum is not secreted in this species). Large males obtain more matings from all three categories than small males. This is because, for each category of mating, females are initially unwilling to court. When a female is mate-guarded prior to her receptivity, she encounters the male frequently, and upon becoming receptive begins courting without aggression. Conversely, when a male encounters a non-pregnant female, or one without young he immediately attempts to court. The male grabs (or attempts to grab) the female's claws and stings her (Benton, 1990). Indeed, the start of a courtship (without mate-guarding) is indistinguishable from a cannibalistic attack. Large males are better at mating with these unwilling females as, unusually for scorpions, large males can be larger than females. In this species, and others (Polis, 1980), size (especially claw-size) is a good predictor of the outcome of cannibalistic contests. At the start of courtship, males
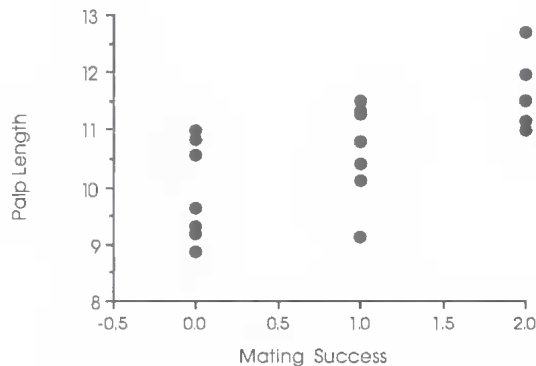
FIG. 2. Relationship between size (claw-length) and mating success in laboratory males free on wall surface (mean ± SD). Difference between groups is significant (Kruskal-Wallis, H=11.4, P=0.003).

sting females, and larger males can eat adult females (and often do: 10 cases observed in the laboratory), therefore, large males essentially give females the choice of being cannibalised or accepting courtship. Small males obtain fewer matings as they have a smaller (or nonexistant) size-advantage over females (Fig. 3) and therefore are more likely to flee from those females who are not immediately willing to court.

SIZE DIMORPHISM

Sexually mature adult males are recognised by the secondary sexual characteristic of a notch in the pedipalpal fingers (Fig. 3). Adult males can differ markedly in size, and this is especially noticeable when one considers claw size, which increases allometrically with body size, such that larger males have disproportionately larger claws (Fig. 3). The frequency distribution of adult male claw sizes at Sheerness was dimorphic (Fig. 4). This dimorphism also occurs with other measures of size, such as prosoma length (Benton, 1991b). This dimorphism probaly arises because there are two instars of adult male in the population at Sheerness: 6th and 7th (see also Benton, 1991b).

DISCUSSION

Two points are noteworthy. Firstly, the reproductive ecology of *Euscorpius flavicaudis* is much more complex than previously imagined. Naively placing pairs of scorpions together in a laboratory situation to watch the courtship would present a very misleading picture because the most significant behaviours occur before actual courtship. Precopulatory mate-guarding has not
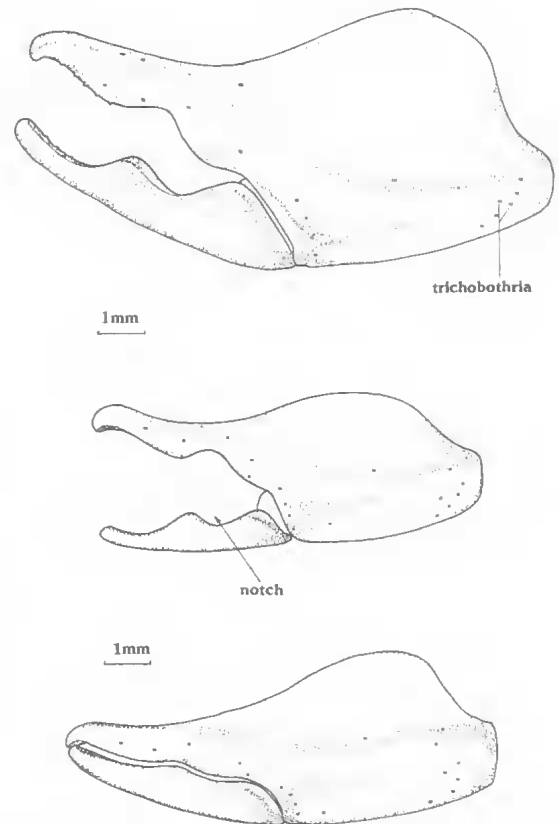

FIG. 3. Claws of two adult ♂ ♂ (a, b) and one adult ♀ (c) same scale. Note secondary sexual characteristic: notch in fingers.

been reported in scorpions, but is known to occur in some spiders (e.g. Vollrath, 1980; Watson, 1990) and occurs widely across the animal kingdom (Ridley, 1983). For precopulatory mate-guarding to evolve, males must gain an advantage by staying with a female prior to her becoming receptive rather than searching for a receptive female. Two criteria may determine this situation: firstly, if a male can predict when a female is going to become receptive, and, secondly if receptive females are difficult to find. The former may occur if females become receptive following a moult (e.g. Watson, 1990), or as in the case of these scorpions, after maternal care. The latter criterion may result from female receptivity being very limited in time (e.g., in *Gammarus* female receptivity is limited to a brief period between moulting and the hardening of the amphipod's exoskeleton: Grafen and Ridley, 1983), low population densities (and so low encounter rates) or because of high male mortality
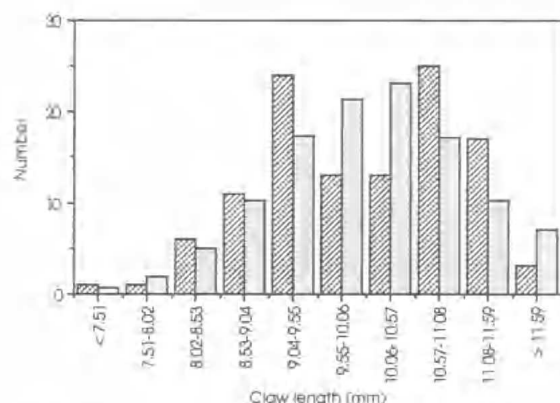
FIG. 4. Distribution of claw-sizes in adult ♂ ♂ is significantly non-normal. Filled bars are observed distribution; stippled bars are expected normal distribution given mean and standard deviation of data. (χ^2=21.1, P<0.005).

during mate-searching (Vollrath, 1980). The period of female receptivity is reduced where the paternity of a male is ensured by being the first male to mate with a female (so called first-male sperm priority), which may be common in arachnids (e.g. Vollrath, 1980; Watson, 1990). A virgin female is far more valuable to a male than one which is already mated. Thus, *Euscorpius flavicaudis*, first-male sperm-priority and low population densities, coupled with the female's receptivity being predictable, may make it more profitable for a male encountering a female engaged in maternal care to mate-guard her rather than risk searching for another female nearer receptivity.

Secondly, there seems to be a paradox. Adult males exist as two instars in the population. This itself is not a novel finding (see Francke and Jones, 1982). It is surprising that any males mature at the smaller instar since the smaller males seem to be at such a disadvantage in obtaining mates. Natural selection would quickly eliminate any tendency to mature at a disadvantageous size.

The paradox suggests two explanations. First, large males may have an advantage only in a mating season. As large males have more instars, they probably take longer to mature. Although males mate more in the short-term, the younger they mature presumably the more seasons in which to find mates. Perhaps there is a mixed evolutionarily stable strategy (ESS) such that the short-term gains enjoyed by 'large males' are offset by the losses due to having one less season in which to mate, so that, on average, the lifetime reproductive success of 'large' and 'small' males

is equal. This ESS could be maintained by frequency dependent selection (Benton, 1992b): large males do relatively better when rare (as they suffer little competition) so their frequency is increased in the population by natural selection. However, when large males are common their gains are reduced, because of increased competition between them, to a point where they are offset by the cost of delaying maturity. Hence, an evolutionary equilibrium is reached between the genes controlling maturation at the 6th and 7th instars.

Secondly, an alternative explanation for this paradox is that there may be phenotypic plasticity in the maturation stage. A gene that can produce a variety of phenotypes depending on the environment is said to exhibit phenotypic plasticity (Lessels, 1991). The 'optimal' time at which to mature may depend on factors such as food availability, and thus growth rate (Stearns and Koella, 1986). For example, if food is plentiful, and an individual is large for its cohort it may be best to mature early. Conversely, if an individual is small for its cohort then it may be better to delay maturity until more food is encountered. This seems to be the case in many spiders (e.g., Deevey, 1947; Vollrath, 1980). This subject will be discussed further elsewhere (Benton, in preparation).

LITERATURE CITED

BENTON, T.G. 1990. 'The behaviour and ecology of scorpions.' (Unpublished Ph.D. thesis, University of Cambridge.)

—— 1991a. Reproduction and parental care in the scorpion, *Euscorpius flavicaudis*. Behaviour 117: 20-28.

—— 1991b. The life history of *Euscorpius flavicaudis* (Scorpiones, Chactidae). Journal of Arachnology 19: 105-110.

—— 1992a. Determinants of male mating success in a scorpion. Animal Behaviour 43: 125-135

—— 1992b. The ecology of *Euscorpius flavicaudis* in England. Journal of Zoology, London 226: 351-368.

BIRULA, A.A.B. 1917. 'Scorpions: Fauna of Russia and adjacent countries; Arachnoidea, Volume 1: Scorpiones.' (Petrograd: translated from the Russian by the Israeli Programme of Scientific Translation, Jerusalem, 1965).

DEEVEY, G.B. 1949. The developmental history of *Latrodectus mactans* (Fabr.) at different rates of feeding. American Midland Naturalist 42: 189-219.

GRAFEN, A. & RIDLEY, M. 1983. A model of mate guarding. Journal of Theoretical Biology 102: 549-567.

FAGE, L. 1928. Remarques sur la dispersion en France et l'acclimation en France de l' *"Euscorpius flavicaudis"* (De Geer). Association Francais pour l'avancement des sciences, La Rochelle 1928: 650-652.

FRANCKE, O.F. & JONES, S.K. 1982. The life history of *Centruroides gracilis* (Latreille). Journal of Arachnology 9: 223-239.

LOURENCO, W.R. & VACHON, M. 1981. Complements à la description d'*Acanthrothraustes brasiliensis* (Mello-Leitão, 1931) (=*Teuthraustes brasiliensis* Mello-Leitão, 1931), synonyme d'-*Euscorpius flavicaudis* (Geer, 1778) (Scorpiones, Chactidae). Journal of Arachnology 9: 223-228.

LESSELS, C.M. 1991. The evolution of life histories. Pp. 32-68. In Krebs, J.R. and Davies, N.B. (eds.) 'Behavioural Ecology: an evolutionary approach'. 3rd Edition. (Blackwell Scientific Publications: Oxford).

MACHAN, L. 1968. Spectral sensitivity of scorpion eyes and the possible role of shielding pigment effect. Journal of Experimental Biology 49: 95-105.

POLIS, G.A. 1980. The significance of cannibalism on the demography and activity in a natural population of desert scorpions. Behavioural Ecology and Sociobiology 7: 25-35.

RIDLEY, M. 1983. 'The explanation of organic diversity.' (Clarendon Press: Oxford).

STEARNS, S.C. & KOELLA, J.C. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. Evolution 40: 893-913.

VOLLRATH, F. 1980. Male body size and fitness in the web-building spider *Nephila clavipes*. Zeitschrift für Tierspsychologie 53: 61-78.

WANLESS, F.R. 1977. On the occurrence of the scorpion *Euscorpius flavicaudis* (DeGeer) at Sheerness Port, Isle of Sheepey, Kent. Bulletin of the British Arachnological Society 4: 74-76.

WATSON, P. J. 1990. Female-enhanced male competition determines the first male and principle sire in the spider *Linyphia litigiosa*. Behavioural Ecology and Sociobiology 26: 77-90.